

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

THE EPIMERA OF NORTH AMERICAN FRESH-WATER
SPECIES OF *GAMMARUS* (CRUSTACEA:
AMPHIPODA) ¹

BY GERALD A. COLE

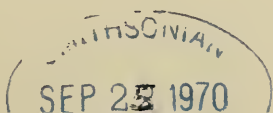
*Dept. of Zoology, Arizona State University,
Tempe, Arizona*

Taxonomic difficulties inherent in making specific identifications of gammarid amphipods are notorious. The perplexing variations among instars and size classes, sexual dimorphism, the difference between summer and winter populations, the lack of systematic importance associated with the genitalia, overlapping ecological and geographic ranges, and the morphological differences between isolated conspecific populations are well known (Sexton, 1924; Bousfield 1958, 1969; Holsinger 1967; Nijssen and Stock 1966; Minckley and Cole 1963).

Workers studying the Nearctic, fresh-water amphipods owe a great debt to Bousfield (1958), who first applied the subtle refinements of European taxonomists to the North American fauna. Despite this, difficulty persists in correctly identifying the species of *Gammarus* found in fresh waters of this continent. For example, *Gammarus minus* Say is confused with at least *G. pseudolimnaeus* Bousfield, *G. troglophilus* Hubricht and Mackin, *G. pecos* Cole and Bousfield, and *G. lacustris* G. O. Sars. The long standing uncertainty concerning the status of *G. fasciatus* Say and *G. tigrinus* Sexton is documented by Hynes (1954), Hynes *et al.* (1960) and Bousfield (1958, 1969).

Structures that rarely have been detailed in depth, even

¹ The financial support received from the University Grants Committee, Arizona State University, is acknowledged with gratitude. I am further indebted to Dr. Thomas E. Bowman, Dr. John R. Holsinger, and Dr. E. L. Bousfield for the loans of *G. fasciatus*, *G. acherondytes*, and *G. duebeni* material, respectively.



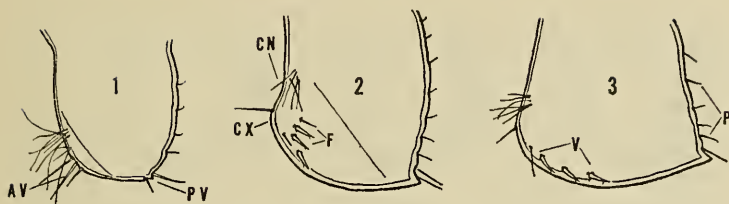
though they serve in specific identification, are the epimera of the first three abdominal segments of North American *Gammarus* species. These have been termed variously as abdominal side plates, epimeral plates, metasomal plates, or epimera. For the species occurring in North American fresh and brackish waters, good figures of all three plates exist only for *G. tigrinus* (Sexton 1939, Figs. 18, 19, 22), *G. lacustris limnaeus* (Bousfield 1958, Fig. 9), *G. minus* (Shoemaker 1940, Fig. 2, j), *G. bousfieldi* (Cole and Minckley 1961, Figs. 13, 14, 15), *G. pecos* (Cole and Bousfield 1970, Figs. 22, 23, 24), and the recently described *G. daiberi* (Bousfield 1969, Fig. 1) which ecologically approximates *G. tigrinus*. This is unfortunate because, despite expected individual variation and slight sexual dimorphism, there are many instances where shape and armature of the abdominal side plates serve to distinguish and separate morphologically similar species that are puzzling to the non-specialist.

It is the purpose of this report to describe in detail the abdominal side plates of the named Nearctic fresh-water species of *Gammarus*, and the oligohaline-brackish water *G. tigrinus*.

The euryhaline *G. duebeni* Lilljeborg (Figs. 1-3) is used to illustrate general features of the three epimera. This species occurs, on this continent, in tide pools and tidal fresh waters from southern Labrador to Massachusetts (Bousfield 1958). Within this geographical and ecological range there is no fresh-water species with which it could be confused, although its abdominal side plates closely resemble those of *G. minus*. *G. duebeni* will be discussed later and briefly with the latter.

GENERAL DESCRIPTION OF THE EPIMERA

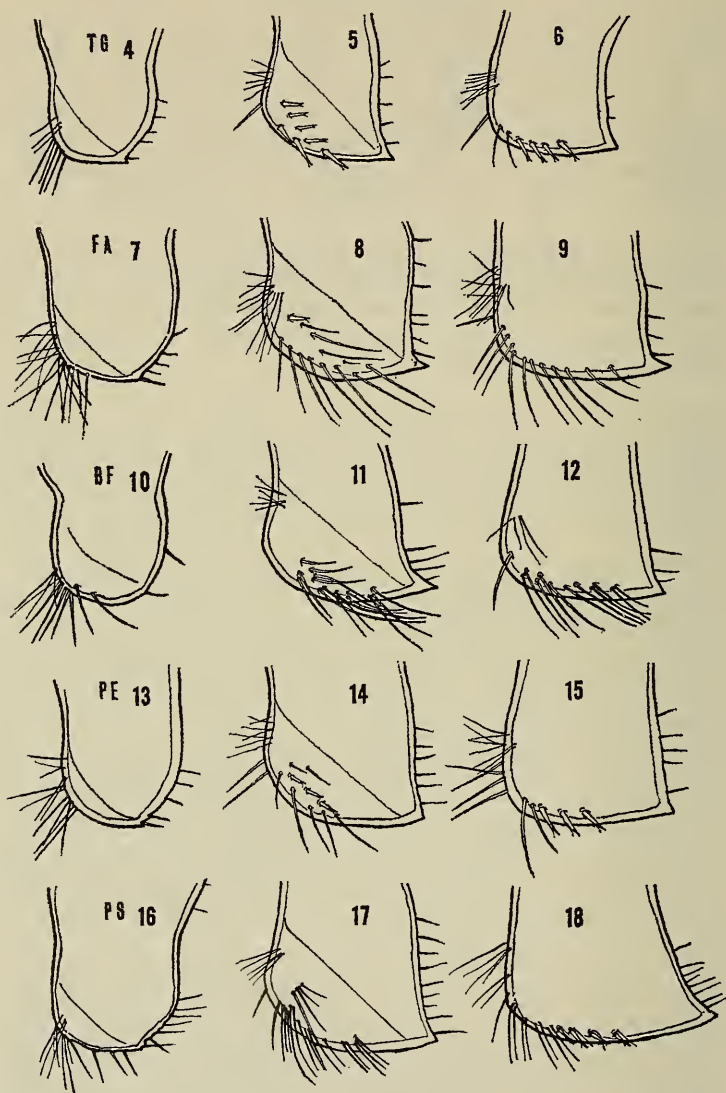
Epimeron I (Fig. 1) is more or less rounded with a faint diagonal chitinous line running from the antero-proximal region to the postero-ventral region. The ventral margin may vary individually; in most species it is nearly straight, appearing truncate. Anterior setae are inserted near the antero-ventral angle (Fig. 1, AV); they become stouter near the angle where they are mostly marginal in origin. These stout setae usually originate in notches. In some instances there may be a short,



FIGS. 1-3. Epimera of male *Gammarus duebeni*, Jewer Cove, Nova Scotia. 1. First epimeron; AV, antero-ventral setae; PV, postero-ventral angle and setae. 2. Second epimeron; CN, proximal concavity; CX, anterior convexity; F, facial armature. 3. Third epimeron; V, submarginal ventral armature; P, posterior setae.

spinellike seta at the antero-ventral angle. In most species there are marginal, ventral setae close to the antero-ventral corner, and no more than one third of the ventral margin is clothed; there are specific exceptions to this. There are no facial setae inserted above the ventral items on epimeron I. The postero-ventral angle (Fig. 1, PV) is usually marked by a sharp notch from which a seta arises. In those specimens with a truncate first epimeron, an angular appearance is imparted by the notch. The posterior margin is convex and armed with relatively short setae.

Epimeron II (Fig. 2) is marked anteriorly by a proximal concavity (Fig. 2, CN) followed by a broad convexity (Fig. 2, CX) that is part of the rounded antero-distal angle. The ventral surface is relatively straight or faintly convex and the postero-ventral corner is either quadrate, slightly produced and acute, or conspicuously produced. The posterior margin is either straight, oblique, or somewhat sinuate. A thickened line of chitin runs from the antero-proximal region to the postero-ventral angle. In most species there are hairlike setae in the anterior concavity, inserted marginally or slightly submarginally. These submarginal setae usually arise from the inner surface of the plate. Slender, straight setae may be borne marginally on the anterior convexity. The ventral setae and spines are submarginal in origin, inserted in most species within the anterior half of the plate; in others they extend nearly to the posterior angle. The ventral spines and setae are some-



FIGS. 4-18. TG 4, 5, 6. Epimera of male *Gammarus tigrinus*; pond near Moonstone Beach, South Kingstown, Washington Co., Rhode Island. FA 7, 8, 9. Epimera of male *Gammarus fasciatus*; Delaware River, N. of Riverton, Burlington Co., New Jersey. BF 10, 11, 12. Epimera of male *Gammarus bousfieldi*; Doe Run, near Ekron, Meade Co., Kentucky. PE

times inserted singly; in other species they may occur in groups, items of each group originating closely in vertical rows. Facial spines and/or setae (Fig. 2, F) are characteristic of epimeron II. Facial items may be inserted singly or in groups, depending on species. A few slender, posterior setae originate marginally, the distal one being very near the postero-ventral angle.

Epimeron III is somewhat broader than the preceding and this is pronounced in certain species. The proximal anterior concavity is shallower than that of epimeron II, and there is no diagonal structure such as those evidenced in epimera I and II. The ventral border is straight or weakly convex. The postero-ventral corner is acute or produced in most species. Hairlike setae originate at the shallow anterior concavity; in some species these are very rare. The antero-distal convexity sometimes bears marginally inserted, slender, straight setae; in some species it is naked, or the setae at this region are distinctly submarginal. The ventral armature (Fig. 3, V) is submarginal and extends posterior to the midway mark in a few species. Ventral insertions may be single or multiple. Facial armament occurs on this plate very rarely. The setae lining the posterior margin (Fig. 3, P) of epimeron III are usually numerically inferior to those of epimeron II.

SPECIFIC DESCRIPTIONS OF THE EPIMERA

Gammarus tigrinus Sexton

(Figs. TG 4, 5, 6)

This species occurs in brackish and tidal fresh waters along the Atlantic coast from the north shore of the Gulf of St. Lawrence to North Carolina with a Florida population in the St. John's River and estuary; it co-occurs with a sibling species *G. daiberi* Bousfield in the Chesapeake-Delaware Bay region (Bousfield 1969). Apparently it has been introduced to England, Ireland (Bousfield 1958, Hynes *et al.* 1960), Germany (Schmitz 1960) and the Netherlands (Nijssen and Stock 1966). Although probably native to the east coast of North America, it was first recognized as a distinct species in material collected in Worcestershire, England (Sexton 1939).

←

13, 14, 15. Epimera of male *Gammarus pecos*; Willbank Spring, Fort Stockton, Pecos Co., Texas. PS 16, 17, 18. Epimera of male *Gammarus pseudolimnaeus*; Elm Spring, Pine Hills area, Union Co., Illinois.

Several good taxonomic references are available for *G. tigrinus*. They are: Sexton (1939); Bousfield (1958, 1969); Hynes *et al.* (1960); and Nijssen and Stock (1966).

Epimeron I (Fig. TG 4). Anterior surface with eight to 15 slender setae; two to five are submarginal, singly inserted or in groups of two or three continuous with the stouter, spaced, marginal setae near and at the antero-ventral angle. Ventral margin fairly straight and unarmed. Postero-ventral angle conspicuously notched; posterior margin with three to five rather short setae.

Epimeron II (Fig. 5). Anterior concavity with three to 13 hairlike slightly submarginal setae. Slender straight marginal setae inserted distally on the antero-ventral convexity, lead to the angle near where the submarginal ventral insertions commence. Ventral armature consisting of mixed setae and spines, or all spines clothing the anterior half of the plate and set singly; spines protruding beyond the distal margin of the plate. Facial items include four to nine single insertions, forming a sharply oblique row of setae and spines, or of spines alone, leading postero-ventrad to become continuous with the ultimate or penultimate ventral item. Postero-ventral corner quadrate or with slight production; posterior margin bears three to seven short setae.

Epimeron III (Fig. 6). Up to 12 fine, hairlike submarginal setae in the anterior proximal region, and more distally one to four slender, straight setae on the margin of the anterior convexity. The latter set singly and confluent with the submarginal ventral series. Ventral armature with up to eight setae and spines, set singly and clothing more than half the distal border. Postero-ventral angle quadrate or with slight production; posterior margin bears two to five setae.

Discussion: Sexton's figures (1939, Figs. 18, 19, 22) of the abdominal side plates are at odds with the present account. As Bousfield (1958) noted, the North American material he examined revealed nearly quadrate corners, although Sexton described and portrayed the second and third plates with prominent postero-ventral production. Sexton also showed longer posterior setae on the plates, especially the third, than I have figured here. Nijssen and Stock (1966) have shown that younger mature males of this species do not exhibit many of the features "characteristic" of *G. tigrinus*. Sexton's figure of an entire male (1939, Plate IV) was based on a November specimen; I examined June material only, and this may explain some discrepancies. In most instances, the oblique row of facial spines beginning rather high, leading to and confluent with the penultimate or ultimate ventral spine seems to be diagnostic.

Gammarus fasciatus Say
(Figs. FA 7, 8, 9)

According to Bousfield (1958, 1969), *G. fasciatus* occurs in the lower tidal and non-tidal reaches of Atlantic rivers and streams from the St. Lawrence south to the Chesapeake drainage. It is present in the Great

Lakes (see Clemens 1950) and occurs, perhaps, in the Mississippi system. The best taxonomic references to this species are those of Bousfield (1958, 1969).

Epimeron I (Fig. FA 7). As many as 32 anterior setae, usually marginal. At the antero-distal corner setae stouter and arise from notches. Usually no ventral setae, although at times one or two setae close to the antero-ventral corner originate within and clothe approximately the anterior one-fourth of the plate. The postero-ventral notch bearing a seta stouter than the other posterior setae; they total four to six.

Epimeron II (Fig. 8). Up to 12 hairlike setae slightly submarginal in the anterior concavity. Antero-ventral convexity with three to six straight, slender setae marginally inserted. Submarginal ventral setation starting far anteriorly in the antero-ventral angle region, extends almost to posterior margin. Six to eight main ventral insertions, composed of up to 12 long setae; in some individuals these are in close-set vertical groups of two or three. Facial items composed of all setae, a mixture of spines and setae, or all spines; a total of five to seven diagonal or subparallel insertions begin above or anterior to the first ventral setae and lead toward the more posterior ventral setae. The postero-ventral corner usually sharply produced; there are five to nine posterior setae.

Epimeron III (Fig. 9). Anterior concavity with up to 15 hairlike setae, slightly submarginal, single or in groups of three or four; one to five distal setae, spaced and marginal lead to the antero-ventral corner. Ventral armature with up to 11 submarginal, long setae clothing at least three-fourths of the distal margin beginning high and far forward in the antero-ventral region and extending almost to the produced postero-ventral corner. The posterior border lined with two to five setae. Spines usually absent from this plate.

Discussion: Difficulties in distinguishing between *G. tigrinus* and *G. fasciatus* in coastal areas, where their habitats overlap or are contiguous, can be overcome by comparing the epimera. Although *G. tigrinus* may have some facial and ventral setae on epimeron II (not shown in Fig. 5), the extreme setation typical of *G. fasciatus* is not achieved. Furthermore spines are common ventral elements of epimeron III of *G. tigrinus*, but are extremely rare on the setose third plate of *G. fasciatus*.

Gammarus bousfieldi Cole and Minckley
(Figs. BF 10, 11, 12)

Gammarus bousfieldi is known only from the upper reaches of a cave stream in Meade Co., Kentucky, where it coexists with a population of aberrant *G. minus*. Cole and Minckley's original description (1961) contains the only figures of this species. Further notes on its ecology are found in Minckley and Cole (1963), and its affinities are discussed by Cole and Bousfield (1970).

Epimeron I (Fig. BF 10). A short, rounded plate with seven to 12 anterior setae, close-set or in groups of two near the antero-ventral corner; they are stouter near the angle and originate from fine notches. Ventral surface rounded, bearing one to three submarginal setae usually clothing the anterior half only; occasionally the most posterior seta near the postero-ventral angle. Posterior margin with two or three setae.

Epimeron II (Fig. 11). Anterior concavity with three to six submarginal, hairlike setae. The antero-ventral convexity bare. Ventral submarginal setation including single setae and groups of two or three, totaling up to 18 setae; more than half the ventral margin clothed. Facial items consist of long setae, singly or in groups of two to five in vertical rows; there are two or three groups. The postero-ventral corner produced and three to six long setae on posterior margin. No spines occur on this plate.

Epimeron III (Fig. 12). Anterior margin with three to eight small submarginal setae at or slightly distal to the anterior concavity. The antero-ventral convexity unarmed except for a straight submarginal seta, which may belong to the ventral series. Ventral armature with up to 20 long setae, arising singly or in vertical groups of two and extending caudad at least midway and usually almost to the postero-ventral corner. The postero-ventral angle somewhat produced; two to four long setae on the posterior border.

Discussion: *G. bousfieldi* is unique because there are no spines on its plates. In some specimens of *G. fasciatus* this may also apply, but the two species differ in their first epimera, and because *G. fasciatus* has much more anterior and antero-ventral setation. The few ventral setae on the first plate of *G. bousfieldi*, and the seta at the anterior convexity of epimeron III are unique in originating submarginally.

Gammarus pecos Cole and Bousfield
(Figs. PE 13, 14, 15)

This species is known from a limnocrone and spring brook near Fort Stockton, Pecos Co., Texas. Other gammarids occur within the Pecos River drainage system north to at least Roswell, Chaves Co., New Mexico; these are of uncertain status but are closely related to *G. pecos* and obviously were derived from the same stock. The original description of *G. pecos* (Cole and Bousfield 1970) is the only published taxonomic reference available.

Epimeron I (Fig. PE 13). Anterior surface with eight to 13 fine setae, mostly marginal and singly inserted; proximal setae sometimes in groups of two or three. The more distal setae stouter, lead to the antero-ventral corner. Usually no ventral setae, but sometimes one to three setae occupying marginal notches within anterior half of the ventral margin. The postero-ventral corner usually notched and the posterior edge supports three to seven relatively long setae.

Epimeron II (Fig. 14). Anterior concavity with eight to 10 hairlike setae; first two or three marginal, subsequent insertions submarginal single and paired. Anterior convexity with two or three slender straight setae spaced and inserted marginally. Ventral submarginal armature of three to seven items inserted singly; spines and setae arise from the anterior half of the plate. Facial armament of three to five single spines and setae (rarely as many as seven), diagonally arranged or sub-parallel to antero-ventral curve and leading toward penultimate or ultimate ventral item. Postero-ventral angle quadrate or produced; the posterior margin bears four to eight relatively long setae.

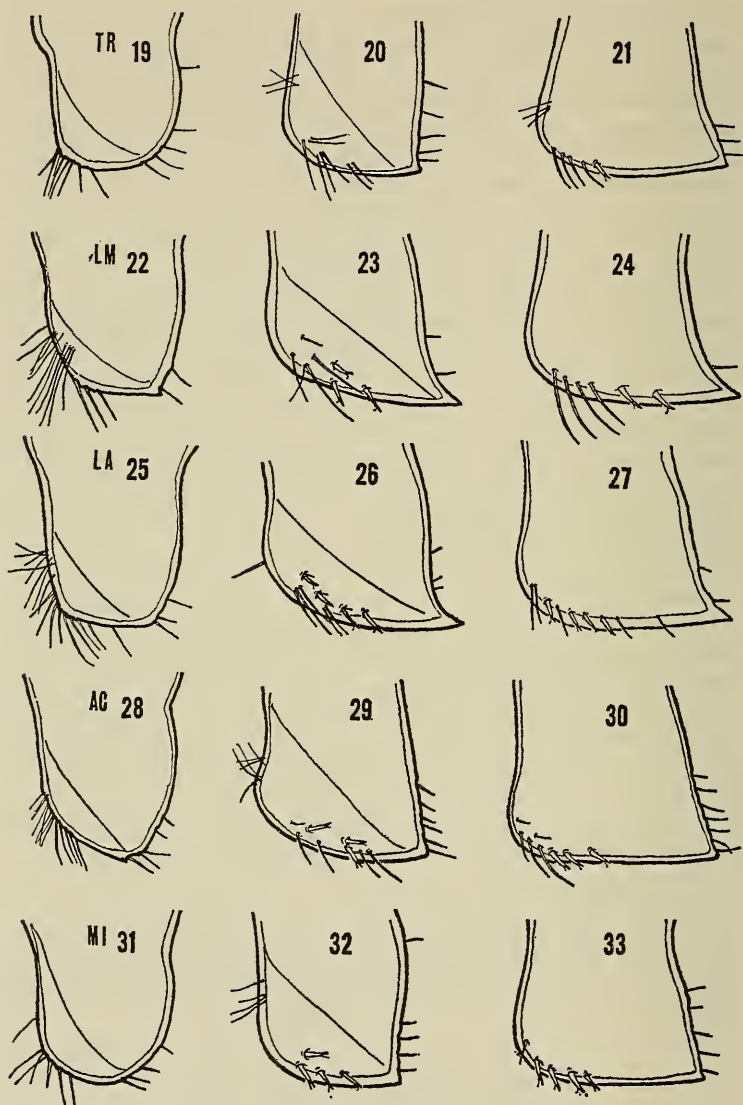
Epimeron III (Fig. 15). Up to 11 long hairlike setae in the anterior concavity; proximal setae arise marginally, distal items originate submarginally, single and paired. One to four marginal, spaced, slim setae lead to the antero-ventral corner. Ventral submarginal armature includes four to six spines and long setae inserted singly and only in anterior half of the plate; armature may consist of mixed spines and setae, all spines, or all setae. Rarely one or two slim facial setae inserted singly in the region of the penultimate ventral item. The postero-ventral angle quadrate or moderately produced; the posterior border bears four to seven relatively long setae.

Discussion: The four species discussed to this point have served to blur distinctions between the subgenera *Gammarus* and *Rivulogammarus* (Cole and Minckley 1961; Cole and Bousfield 1970). In life they are conspicuously banded, and on the basis of other morphological features they seem to be closely related. They show certain similarities in their epimera; in this sense, *G. tigrinus* is much like *G. pecos*, and the origin of the latter from a *G. tigrinus*-like ancestor is not unreasonable. *G. bousfieldi* and *G. fasciatus* possess much more setose epimera than do the other two species, and have more produced postero-ventral corners of epimeron II and III than do the others. In all four species the facials of epimeron II are diagonally arranged and lead toward the penultimate or ultimate ventral items; this is especially marked in *G. tigrinus* and least in *G. bousfieldi*.

It is noteworthy that in addition to the linking of the two subgenera, *Gammarus* and *Rivulogammarus*, by intermediate species, there are nomenclatural technicalities calling for the rejection of the latter (Stock 1969).

Gammarus pseudolimnaeus Bousfield
(Figs. PS 16, 17, 18)

This gammarid is common in the Mississippi drainage and the southwestern St. Lawrence system (Bousfield 1958). It occurs in large rivers, lakes and their tributary streams, springs, rheocrenes, and cave streams. It coexists in appropriate areas with *G. fasciatus*, *G. troglophilus*, and *G. minus*; in small springs of the Pine Hills region, Union Co., Ill., it co-



FIGS. TR 19, 20, 21. Epimera of male *Gammarus troglophilus*; Elm Spring, Pine Hills area, Union Co., Illinois. FIGS. LM 22, 23, 24. Epimera of male *Gammarus lacustris limnaeus*; Grand Lake, St. Louis Co., Minnesota. FIGS. LA 25, 26, 27. Epimera of male *Gammarus lacustris lacustris*; spring in Adobe Valley, Mono Co., California. FIGS. AC 28, 29, 30.

occurs with the last two species simultaneously. It has been confused with several species, both before and after Bousfield recognized its specific status. His paper (Bousfield 1958) is the only publication with figures and other taxonomic aids concerning this widespread form.

Epimeron I (Fig. PS 16). Up to 20 close-set anterior setae, at times arising rather high on the plate. The proximal setae submarginal, the distal setae stouter and marginal; the antero-ventral angle may bear a short spinelike seta arising from a notch. The ventral edge rounded, bears three to eight well spaced setae originating from notches; the entire border usually clothed. The posterior margin bears three to eight relatively long setae.

Epimeron II (Fig. 17). Anterior concavity with four to 10 submarginal hairlike setae. The antero-ventral convexity sometimes bears a slender, marginal seta, but usually no marginal antero-ventral setae. Submarginal ventral armature with 11–20 long setae, set singly and in vertical groups; these begin in the antero-ventral region; spines very rare on this plate. Facial armature includes five to nine setae singly or in groups of two to four, arranged diagonally; the anterior facial items starting roughly above the third ventral item. The postero-ventral angle usually unproduced; five to 10 long posterior setae.

Epimeron III (Fig. 18). Anterior concavity with four to 10 hairlike setae, mostly submarginal. On the antero-ventral convexity one to five singly inserted or paired straight setae. Submarginal ventral armature consisting of two to six groups starting far forward; the anterior items may be paired or single setae, the posterior items are spines, each accompanied by a short seta. Ventral armature investing approximately the anterior half, or less. The postero-ventral corner produced more than epimeron II, and there are two to eight long posterior setae.

Discussion: *G. pseudolimnaeus* is characterized by the first epimeron being clothed by ventral setae, a setose second epimeron that rarely bears spines and, uniquely, a third plate with ventral spines, each of which is accompanied by a short seta. Its second plate is much like that of *G. bousfieldi*; its first plate is intermediate between those of *G. fasciatus* and *G. bousfieldi*; its third plate is uniquely armed.

Gammarus troglophilus Hubricht and Mackin
(Figs. TR 19, 20, 21)

The exact range of this species is not known; it is relatively common south of Wisconsin glaciation limits in Illinois and Missouri. It is present in cave streams, springs and rheocrenes, where it may co-occur with *G.*

←

Epimera of male *Gammarus acherondytes*; Morrison's Cave, Burksville, Monroe Co., Illinois. Figs. MI 31, 32, 33. Epimera of male *Gammarus minus*; Morgan's Creek, Otter Creek Park, Meade Co., Kentucky.

pseudolimnaeus, *G. minus*, or *G. acherondytes*. The papers of Hubricht and Mackin (1940) and Bousfield (1958) are the best taxonomic references to *G. troglophilus*.

Epimeron I (Fig. TR 19). Five to eight anterior strong setae near the antero-ventral corner, usually inserted singly although some proximal setae may be paired; stoutest setae at the corner and in faint notches; sometimes a spinelike seta present at the angle. Setae continue on to no more than the anterior third of the straight or broadly rounded ventral margin. The posterior border with two to six long setae.

Epimeron II (Fig. 20). Anterior concavity with two to five fine submarginal setae, often arising in a vertical series. Antero-ventral convexity and angle naked. Ventral submarginal armature consisting of two or three groups of setae arranged in vertical series, or spines each with a long seta directly above it. Ventral insertions not extending beyond the anterior half of the plate. The facial setae include one or two insertions, sometimes double and close to the ventrals, especially posteriorly. The postero-ventral angle quadrate or slightly produced. Relatively long setae (two to six) line the posterior margin.

Epimeron III (Fig. 21). Anterior concavity with two to four hairlike setae inserted submarginally and vertically arranged, singly or in groups of two. Ventral items include three to six submarginal insertions extending caudad less than half the breadth of the broad plate; armature consisting of long setae and spines, usually mixed, rarely only setae are present; setae occasionally in pairs vertically arranged. Rarely a slender seta or a spine inserted facially midway between the penultimate and ultimate ventral items. Slight production of the postero-distal corner; the posterior border bears two to four setae. This plate markedly broader than epimeron II.

Discussion: Probably *G. troglophilus* is most often confused with *G. pseudolimnaeus*. The latter species has more setose abdominal side plates and is always distinguishable by the ventral armature of the third plate.

Gammarus lacustris limnaeus S. I. Smith
(Figs. LM 22, 23, 24)

Gammarus lacustris lacustris G. O. Sars
(Figs. LA 25, 26, 27)

The nomenclature here follows Bousfield (1958) who designated the populations in the St. Lawrence drainage basin as *G. l. limnaeus*, and those in the Hudson Bay drainage, western North America, and northwestern Europe as *G. l. lacustris*. Whether this is a polytypic species or two distinct species is not explored here. The variations shown among the figures portraying epimera of *G. l. limnaeus* and *G. l. lacustris* are not much greater than can be found among different populations of a single species, although *G. l. limnaeus* may be more setose than the latter. Discussions and figures of this species or species complex have appeared in

the literature since the late 19th Century, but the best modern taxonomic aids are the papers of Bousfield (1958) and Hynes *et al.* (1960).

Epimeron I (Figs. LM 22, LA 25). Anterior surface with up to 20 relatively strong setae inserted singly and in groups of two to four, marginal and submarginal. The distal setae sometimes set in notches and leading to the antero-ventral corner where they are confluent with the ventral setae. Ventral margin truncate; ventral setae marginal, set in fine notches and usually close to the antero-distal corner. Postero-ventral angle either blunt or with an obvious notch; one to three setae on the posterior margin.

Epimeron II (Figs. 23, 26). No anterior setae or one slender straight submarginal seta arising from the anterior convexity. The ventral armature includes two to eight submarginal insertions, often in groups of two; they clothe about half the distal margin. The ventral armature with spines and setae, the anterior setae being the longest; short setae sometimes accompany the spines. The facial insertions fewer than the ventrals, but include spines and setae, and sometimes paired; facial armature set low above the anterior ventral items. The postero-ventral corner remarkably produced; the posterior margin bears one to five (usually two or three) small setae.

Epimeron III (Figs. 24, 27). Usually no anterior setae, but sometimes one or two slender setae arise from margin of anterior convexity. The ventral armature with spines and setae occupying half or more of the ventral margin; these include three to 10 submarginal insertions, usually single but rarely two setae in a group: no short setae with the spines. The postero-ventral angle remarkably produced; posterior margin bears one to four short setae.

Discussion: The variation seen among epimera in any single species may not be exaggerated in the figures for *G. lacustris limnaeus* (Figs. 22–24) and *G. lacustris lacustris* (Figs. 25–27) although the third plate of the former (Fig. 24) often has longer setae than usually found in *G. l. lacustris*. Whether these represent two species or a single polytypic species is questionable. Hynes *et al.* (1960) show the second and third epimera of *G. lacustris* from England with less production of the postero-ventral corners. Bousfield (1958) portrayed the three epimera of *G. l. limnaeus* with produced corners on the last two plates. He stated (*loc. cit.*, p. 81) that the North American material of *G. lacustris lacustris* has subquadrate or acute, but unproduced abdominal side plates, but that (*loc. cit.*, p. 84) *G. lacustris limnaeus* has acutely produced corners. He also implied variation by stating that lotic-water specimens tend to have more acutely produced abdominal side plates than lentic-water forms.

Gammarus acherondytes Hubricht and Mackin
(Figs. AC 28, 29, 30)

As far as is known, *G. acherondytes* is restricted to cave streams of Monroe Co., Illinois, north of the Illinois Ozarks. It co-occurs with *G.*

troglophilus. The original description by Hubricht and Mackin (1940) and Bousfield's redescription (1958) are the only taxonomic publications on this species.

Epimeron I (Fig. AC 28). Distal anterior surface and antero-ventral angle with seven to 15 setae; the proximal setae in groups of two or three and slightly submarginal; setae near the antero-ventral corner marginal, stouter and set in fine notches. Ventral margin oblique and mostly unarmed. A conspicuous postero-ventral notch and a rather straight posterior margin lined with two to six setae.

Epimeron II (Fig. 29). In the distal part of the anterior concavity zero to six close-set, hairlike setae. The antero-ventral convexity bare. Submarginal ventral armature including three to five singly inserted spines and setae occupying a little more than half of the margin. Facial items include three to seven spines and setae inserted singly and subparallel to ventral margin. The postero-ventral angle acute but unproduced; posterior margin bears two to six setae.

Epimeron III (Fig. 30). No fine setae found in the anterior concavity. Ventral, submarginal insertions include four to six items set singly, commencing near the antero-ventral margin and clothing no more than the anterior half of the broad plate. Anterior ventral items may be setae; the posterior two to four items are spines. One or two small facial setae may occur in the anterior part of the plate. Postero-ventral corner often acute, but not produced; posterior margin with up to eight setae.

Discussion: The first epimeron of this rare species has an unique oblique ventral margin. Its second plate is reminiscent of that of *G. minus*, and its third plate has armature similar to that of *G. troglophilus*, *G. lacustris* and *G. minus*, although shaped like the last.

Gammarus minus Say
(Figs. MI 31, 32, 33)

Apparently *G. minus* is found in an east-west band south of the Wisconsin Glaciation limits and north of the greatest advances of the Eocene Sea during the Mississippi Embayment. It ranges from the Philadelphia and Washington regions west into the Ozark Plateau. Although the species shows pronounced geographical variation, the abdominal side plates seem to be remarkably uniform throughout its range. There are two good descriptions of the species, although based only on eastern specimens (Shoemaker 1940; Bousfield 1958).

Epimeron I (Fig. MI 31). Up to 10 anterior setae, mostly near the antero-ventral corner, set singly and in groups of two, three, or four; proximal setae often slightly submarginal; distal setae marginal spaced and stouter, inserted in notches; sometimes a short, spinelike seta present at the distal corner. Ventral margin rounded or straight; some setae continuous with the antero-ventral setae extend onto the anterior third of the plate; rarely a single seta set in a notch at the midway mark.

Postero-ventral corner sharply notched, or blunt, with one or two setae; posterior margin with one to four setae.

Epimeron II (Fig. 32). Anterior concavity with zero to four submarginal hairlike setae. Antero-distal convexity bare. Ventral submarginal armature usually includes three items set singly, three spines, two setae and a spine or two spines and a seta. Tips of the ventral spines do not, or scarcely protrude past distal margin. Ventral armature may occupy less or slightly more than half the plate's breadth. Facial armature of one or two items, usually a spine, two spines, or a spine and a seta. When one item is present, it is relatively low; the second item anterior and dorsal to it. The postero-ventral corner quadrate or little produced; the posterior setae range from two to eight, rarely more than five.

Epimeron III (Fig. 33). Anterior concavity with zero to five small, slightly submarginal setae. Antero-ventral convexity and angle bare although the first submarginal ventral item may be at that angle. Ventral items, two to five, set singly; anterior ones may be relatively long setae, posterior ones spines, or all of them spines, occupying less than one-half the breadth of the plate. Postero-ventral corner quadrate or very slightly produced; posterior margin with one to five setae.

Discussion: In general, the North American *Gammarus* species can be arranged from the most setose, *G. bousfieldi*, to the least, *G. minus*. The epimera of *G. minus* have the sparsest armature of all species discussed here. In this respect its plates are most like those of *G. acherondytes* and *G. duebeni*. The facial items on epimeron II are especially wanting; in larger specimens a second item is present, although not shown in Fig. 33; Shoemaker (1940, Fig. 2, j) shows this. He stated (*loc. cit.*, p. 390) that the last two plates have "... the lower hind corners sharply produced." His figures show, in my opinion, acute corners with very slight production.

G. duebeni (Figs. 1-3) is probably not to be found within 400 or more km of the nearest *G. minus* population; its epimera, however, are much like those of the latter species. They differ specifically from *G. minus* in having: more posterior setae on all plates; a slender, straight, marginal seta near the anterior convexity in plates II and III; more convex ventral margins of plates II and III; more setae in the anterior concavity of epimeron III; more facial armature on epimeron II; and, that facial armature arranged vertically rather than diagonally.

LITERATURE CITED

- BOUSFIELD, E. L. 1958. Fresh-water amphipod crustaceans of glaciated North America. *Canadian Field-Naturalist* 72: 55-113.
- . 1969. New records of *Gammarus* (Crustacea: Amphipoda) from the middle Atlantic region. *Chesapeake Sci.* 10: 1-17.
- CLEMENS, H. P. 1950. Life cycle and ecology of *Gammarus fasciatus*

- Say. Ohio State Univ. Franz Theodore Stone Inst. Hydrobiol. Contribution 12: i-iv, 1-63.
- COLE, G. A., AND E. L. BOUSFIELD. 1970. A new freshwater *Gammarus* (Crustacea: Amphipoda) from western Texas. Amer. Midl. Naturalist 83: 89-95.
- AND W. L. MINCKLEY. 1961. A new species of amphipod crustacean (Genus *Gammarus*) from Kentucky. Trans. Amer. Microscop. Soc. 80: 391-398.
- HOLSINGER, J. R. 1967. Systematics, speciation, and the distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). U. S. Nat. Mus. Bull. 259: i-vi, 1-176.
- HUBRICHT, L., AND J. G. MACKIN. 1940. Description of nine new species of fresh-water amphipod crustaceans and new localities for other species. Amer. Midl. Naturalist 23: 187-218.
- HYNES, H. B. N. 1954. On the identity of *Gammarus tigrinus* Sexton 1939. Nature 174: 563.
- , T. T. MACAN, AND W. D. WILLIAMS. 1960. A key to the British species of Crustacea: Malacostraca occurring in fresh water with notes on their ecology and distribution. Freshwater Biol. Assoc. Sci. Pub. No. 19, 36 pp.
- MINCKLEY, W. L., AND G. A. COLE. 1963. Ecological and morphological studies on gammarid amphipods (*Gammarus* spp.) in spring-fed streams of northern Kentucky. Occas. Papers Adams Ctr. Ecol. Studies No. 10, 35 pp.
- NIJSEN, H., AND J. H. STOCK. 1966. The amphipod, *Gammarus tigrinus* Sexton, 1939, introduced in the Netherlands (Crustacea). Beaufortia (Amsterdam) 13: 197-206.
- SCHMITZ, W. 1960. Die Einbürgerung von *Gammarus tigrinus* Sexton auf dem europäischen Kontinent. Arch. Hydrobiol. 57: 223-225.
- SEXTON, E. W. 1924. The moulting and growth stages of *Gammarus*, with descriptions of the normals and intersexes of *G. chevreuxi*. Jour. Mar. Biol. Assoc. 13: 340-401.
- . 1939. On a new species of *Gammarus* (*G. tigrinus*) from Droitwich district. *Ibid.* 23: 543-551. Pl. IV, V, VI.
- SHOEMAKER, C. R. 1940. Notes on the amphipod *Gammarus minus* Say and description of a new variety, *Gammarus minus* var. *tenuipes*. Jour. Wash. Acad. Sci. 30: 388-394.
- STOCK, J. H. 1969. *Rivulogammarus*, an amphipod name that must be rejected. Crustaceana 17: 106-107.